CHAPTER 9

Factors Influencing Diversity of Soil Collembola in a Tropical Mountain Forest (Doi Inthanon, Northern Thailand)

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ABSTRACT

Diversity of soil Collembola was examined in five sites of the Doi Inthanon forest (Northern Thailand), in relation to several environmental parameters (altitude, CO_2 in litter, soil temperature, dry weight, organic matter, pH, and granulometry). None of these factors was strongly correlated with species richness at sample points or sites. Removing the 1740- or 2100-m sites improved the correlations of soil and litter Collembolan diversity with several of the parameters. Significant correlations were found between the ratio soil/litter Collembolan diversity and most abiotic factors along the elevational gradient; diversity in soil tended to decrease with altitude, contrary to diversity in litter, which did not display any clear pattern. Accumulation of organic matter at higher elevations was thus associated with lower diversity in soil, which raises the problem of the trophic resources available to soil fauna. Abiotic heterogeneity showed contrasting relationships to species diversity, which led us to distinguish two types of heterogeneity (disturbance heterogeneity and complexity heterogeneity) likely to have opposite influences on community diversity. No direct

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support for the classical productivity or heterogeneity hypothesis relating to species diversity can be drawn from our results. Instead, diversity patterns in the soils of Doi Inthanon seem to be determined by a complex set of factors, and environmental parameters might be more important than trophic parameters.

I. INTRODUCTION

While a profusion of works deals with the relative importance of the higher taxa of Arthropods in tropical soils, analyses of diversity at the species level are poorly documented. Only three papers can be cited for Collembola, in spite of the commonly dominant position of this group in soil communities (Greenslade and Greenslade, 1968): Takeda (1981) investigated the effect of shifting cultivation on Collembolan communities in Eastern Thailand; Betsch and Cancela da Fonseca (1984) studied recolonization of a disturbed forest by Collembola in French Guyana; Deharveng et al. (1989) analyzed the Collembolan diversity of the Doi Inthanon forest in Northern Thailand compared to similar habitats in temperate areas. The papers by Takeda and by Betsch and Cancela da Fonseca relate diversity to the nature and the intensity of man-induced disturbance. Both point to the greater decrease of diversity during the dry season in disturbed habitats as opposed to undisturbed ones. They do not, however, consider the relation of diversity to precise environmental factors, a theme which is embraced in the present chapter.

II. MATERIAL AND METHODS

A. The Study Sites

This study was conducted in the forest of Doi Inthanon (Chiang Mai Province, 18°35'N, 98°29'E). Doi Inthanon, the highest mountain in Thailand at 2590 m, retains large patches of primary forest mainly above 1600 m and below 1000 m on its southeastern slopes. The vegetation in this area has been briefly described by Robbins and Smitinand (1966). Koyama (1984) lists the flora, with detailed vegetation analyses of a quadrat at 1700 m and a transect at 2550 m, which have been sampled for soil fauna in our work.

Five sites were selected at 700, 1700, 1740, 2100, and 2550 m. Four were located in primary rain forest (although some indications of moderate disturbance to soil were seen also at 2100 m), and one (1740 m) was in a disturbed, partially cleared area. At each site, we sampled four points at 1-m intervals. At each point, one sample of litter and one sample of the underlying soil/humus layer (referred to as soil) were made. Each sample had a volume of 500 cm^3; its depth was 5 cm for soil and was variable for litter according to local conditions. All 40 samples were collected on June 1, 1989, at the beginning of the wet season.

B. The Biota (Table 1)

The relative numerical importance of Collembola in tropical soil communities in Thailand increases with elevation whereas termite and ant populations decrease (unpublished observations). In the altitudinal range and in the habitats investigated, these two last groups are unimportant. The dominant soil Arthropods were Acari and Collembola in our material, Collembola outnumbering Acari in 14 of the samples.

The fauna was extracted by Berlese funnel method in Chiang Mai University, then preserved in 90% ethanol. Biota was sorted and counted in Toulouse (France). All Collembola were identified to species level, except some unidentifiable juveniles.

C. The Environmental Variables (Table 2)

Abiotic parameters of proven biological importance for soil Collembola are few (Rusek, 1989; Hagvar and Abrahamsen, 1984). Humidity, temperature, carbon dioxide, pH, and organic matter have been the most frequently studied, and were recorded in our work. Carbon dioxide and organic matter relates to soil productivity and trophic resources for Collembola (mainly fungi and bacteria). Organic matter and pH characterize humus type, which Ponge (1983) has shown to be of primary importance for soil communities. We measured in addition important parameters of the spatial dimension of the niche (relative dry weight, as a measure of the global soil porosity; and granulometry, which contributes to determine the size of the soil pores usable by microarthropods). Carbon dioxide (CO_2, in ppm) was measured with a Gastec pump in the litter. Temperature (temp, in °C) was recorded at -10 cm in the soil to avoid nycthemeral and seasonal variations. Other factors were measured in the laboratory from soil cores. The pH was obtained from soil-water suspension of 10 g/20 mL. Dry weight (dw, in g/1000 cm^3) was measured after complete desiccation without artificial heating. Granulometric analyses were conducted following Baize (1988); coarse elements (between 2 mm and 200 μm), silt (between 200 and 50 μm), and clay (less than 2 μm) were measured in grams per kilogram.

D. Diversity Descriptors (Tables 2, 3, and 4)

Hypothetical abundance distribution models underlying diversity patterns are not considered here. Instead, we undertake an exploratory approach with as few assumptions as possible, using straightforward descriptors of diversity components based on species richness. The appraisal of alpha and beta diversities (Magurran, 1988) is adapted to the scale of our study and to our biological material in the following way:

1. Point diversity (α diversity) is estimated by species richness, i.e., the total number of species in a 500-cm^3 sample (Sl in litter, Ss in soil) or at a sample point (Sls) according to Stanton (1979, p. 302) (Table 2).

Table 1. List of Collembolan Species and Number of Specimens Collected in Soil and in Litter of the Five Sites Studied in Doi Inthanon

	Litter					Soil				
	2550	**2100**	**1740**	**1700**	**700**	**2550**	**2100**	**1740**	**1700**	**700**
Hypogastruridae										
1 *Ceratophysella* n. sp. 1			32	3	2					
2 *Ceratophysella* n. sp. 2			3							
3 *Chinogastrura* sp.	5	13	3	3		2		2		1
4 *Cyclograna* n. sp.	28					12	10			
5 *Xenylla thailandensis* Da Gama, 1986	10	12								
Neanuridae										
6 *Aethiopella* n.sp.	7	2	4	2						
7 *Brasilimeria* n. sp.	1									
8 *Ceratrimeria* sp.			1	1						
9 *Denisimeria caudata* (Denis, 1948)				1						
10 *Friesea* n. sp. 1										3
11 *Friesea* n. sp. 2										2
12 *Friesea* n. sp. 3		1	6	1						
13 *Micranurida pygmaea* Boerner, 1901			63					15		
14 *Neanurinae* n. g. 1, n. sp.			10		2			2		
15 *Neanurinae* n. g. 2, n. sp.							1			
16 *Neanurinae* n. g. 3, n. sp.		1								
17 *Paleonura* n. sp. 1		1	5					2		
18 *Paleonura* n. sp. 2					9				1	3
19 *Paranura meo* Deharveng, 1989		2								
20 *Paranura modesta* Deharveng, 1989		4							1	
21 *Paranura* n. sp.					1					
22 *Pseudachorudina* n. sp. 1	11					3				
23 *Pseudachorudina* n. sp. 2	1									
24 *Pseudachorutinae* n. g., n. sp. 1	1			1		8				
25 *Pseudachorutinae* n. g., n. sp. 2				2						
26 *Siamanura* cf. *gouzei* Deharveng, 1987				2						
27 *Siamanura clavata* Deharveng, 1987				2				2		
28 *Siamanura* n. sp.				1						
29 *Thaianura umeasoi* Yosii, 1961	19	3	3	12					1	

Odontellidae										
30 *Superodontella ciconia* Bedos & Deh., 1990		2		2	1	1	1		19	3
31 *Superodontella flammata* Bedos & Deh., 1990		2								5
32 *Superodontella gouzei* Bedos & Deh., 1990	1						3		10	2
33 *Superodontella longispina* Bedos & Deh., 1990	4	2		4						
34 *Superodontella* n. sp. 1		1								
35 *Superodontella* n. sp. 2	2									
36 *Superodontella* n. sp. 3				1						4
Onychiuridae										
37 *Mesaphorura hygrophila* Rusek, 1971		1								
38 *Mesaphorura* cf. *macrochaeta* Rusek, 1976									2	
39 *Mesaphorura yoshii* Rusek, 1971		5				13	4		5	
40 *Protaphorura* sp.	45	1		50	3	28	3	1	14	54
Isotomidae										
41 *Folsomia* n. sp. 1	4					3				
42 *Folsomia* n. sp. 2	229	9		6		1				
43 *Folsomia* n. sp. 3				27					2	
44 *Folsomides centralis* Denis, 1931				1	6					4
45 *Folsomides exiguus* Folsom, 1932			102	1	8			308	1	17
46 *Folsomides* sp.			2	3				48	4	
47 *Folsomina* n. sp.										6
48 *Folsomina onychiurina* Denis, 1931	2	29		1			13	4	4	10
49 *Isotomiella* n. sp. 1			17		35			9		13
50 *Isotomiella* n. sp. 2									17	1
51 *Isotomiella* n. sp. 3	36	25	23	53		1		1	19	
52 *Isotomiella* n. sp. 4						30	13			7
53 *Isotomiella* n. sp. 5										58
54 *Jestella* n. sp.				14					2	
55 *Micranurophorus* n. sp.						1				
56 *Parisotoma* n. sp.	8									
57 *Parisotoma notabilis* (Schaeffer, 1896)	2									
58 *Proisotoma* n. sp. 1	100									
59 *Proisotoma* n. sp. 2				2		1				
Entomobryidae										
60 *Acrocyrtus* n. sp. 1					12					2
61 *Acrocyrtus* n. sp. 2					6					
62 *Alloscopus tetracanthus* Boerner, 1906					6					32
63 *Alloscopus thailandensis* Mari Mutt, 1985				3						

Table 1. List of Collembolan Species and Number of Specimens Collected in Soil and in Litter of the Five Sites Studied in Doi Inthanon (continued)

	Litter					Soil				
	2550	**2100**	**1740**	**1700**	**700**	**2550**	**2100**	**1740**	**1700**	**700**
64 *Ascocyrtus* n. sp. 1		1								
65 *Ascocyrtus* n. sp. 2					4					
66 *Ascocyrtus* n. sp. 3				6						
67 *Coecobrya* sp.	1		4	3		13		6	14	15
68 *Dicranocentrus fasciatus* Yosii, 1961		30	8	20			2	1	1	
69 *Dicranocentrus* n. sp.	1	2								
70 *Dicranocentrus thaicus* Yosii, 1961	36	34	4	32				1		
71 *Entomobryidae* n. g. 1, n. sp.				1						
72 *Entomobryidae* n. g. 2, n. sp.			4	8	8				3	33
73 *Lepidocyrtus* sp. 1			3		53					5
74 *Lepidocyrtus* sp. 2					2					
75 *Lepidocyrtus* sp. 3	25	34	3	13						2
76 *Lepidocyrtus* sp. 4				1						
77 *Lepidocyrtus* sp. 5		1								
78 *Lepidosira* sp.			4							
79 cf. *Seira* sp.					1					
Paronellidae										
80 *Paronellidae* n. sp.				3						
81 *Paronellidae* sp.				8	1					
82 *Troglopedetes* n. sp.	4	1			10					5
Cyphoderidae										
83 *Cyphoderus* sp.				3						
Oncopoduridea										
84 *Harlomillsia oculata* (Mills, 1937)		1								
Tomoceridae										
85 *Tomocerus* n. sp.	2									
Dicyrtomidae										
86 *Bothriovulsus* n. sp.	7									
87 cf. *Calvatomina* n. sp.					7					
88 *Papiroides* n. sp.					15					
89 *Ptenothrix* n. sp. 1				1						
90 *Ptenothrix* n. sp. 2	5									
91 *Ptenothrix* nr. *brouquissei* Nayrolles, 1989		3	4	5						

Arrhopalitidae										
92 *Arrhopalites* n. sp. 1					1					
93 *Arrhopalites* n. sp. 2			5					2		
94 *Arrhopalites* n. sp. 3	21	1		3		3			2	
95 *Arrhopalites* n. sp. 4	39	26	4	2					1	
Katiannidae										
96 *Sminthurinus* cf. *niger* (Lubbock, 1868)	3									
Sminthuridae										
97 *Neosminthurus* n. sp.	19			29						
98 *Papirinus* n. sp.			1	3						
99 *Pararrhopalites* n. sp.					2					4
100 *Sminthuridae* sp. 1			1							
101 *Sminthuridae* sp. 2			1							
102 *Sphyrotheca* n. sp. 1					19					2
103 *Sphyrotheca* n. sp. 2			6	9						
104 *Sphyrotheca* n. sp. 3	3									
105 *Sphyrotheca* n. sp. 4	20			1						
106 *Sphyrotheca* n. sp. 5	15	1								
Sminthuridae										
107 *Sminthurides* sp.			20							
108 *Sphaeridia* n. spp.	277	65	138	11	65	1		2		
Neelidae										
109 *Megalothorax* cf. *minimus* Willem, 1900					14					2
110 *Megalothorax* n. sp	65	2		4	4		3	1	2	3
111 *Neelides* sp.		4	2							
112 *Neelus* sp.		3	10	14	4					
Number of species	37	35	32	48	28	16	10	17	20	30
Unidentified juveniles										
Friesea sp.					1					
Entomobryidae sp.	1		3		4	1	1	1	1	2
Paronellidae sp.			1		2					
Symphypleona sp.			1	1						1
Total number of individuals	1060	325	501	380	308	122	54	408	125	303

Table 2. Environmental and Diversity Parameters of the 20 Sample Points

	Alt (m)	Temp (°C)	CO_2 (ppm)	DW (g/L)	OM (%)	pH	Coarse (g/kg)	Silt (g/kg)	Clay (g/kg)	Sls	Sl	Ss	Ss/Sl	Cs	Sls/ST	Sl/STl	Ss/STs
1	2550	13.5	300	314.2	50.3	4.6	124	43	433	27	23	9	0.39	0.31	0.64	0.62	0.56
2	2550	13.4	300	274.0	48.9	4.5	117	45	358	24	21	9	0.43	0.40	0.57	0.57	0.56
3	2550	13.5	400	251.2	52.5	4.7	122	41	399	31	26	8	0.31	0.18	0.74	0.70	0.50
4	2550	13.3	400	374.2	39.0	5.0	152	41	333	29	26	7	0.27	0.24	0.69	0.70	0.44
5	2100	15.8	400	375.2	24.8	4.8	328	80	295	19	16	3	0.19	0.00	0.49	0.46	0.30
6	2100	16.0	500	233.4	42.0	4.1	275	67	296	14	12	3	0.25	0.13	0.36	0.34	0.30
7	2100	15.9	650	367.0	30.8	4.9	294	117	294	21	17	5	0.29	0.09	0.54	0.49	0.50
8	2100	15.8	500	310.8	45.4	5.1	208	82	331	26	22	7	0.32	0.21	0.67	0.63	0.70
9	1740	19.2	400	731.0	5.7	6.7	547	177	179	18	16	6	0.38	0.36	0.50	0.50	0.35
10	1740	18.8	400	660.0	4.1	6.0	552	141	207	18	15	7	0.47	0.36	0.50	0.47	0.41
11	1740	18.9	500	m	4.0	6.2	546	182	210	17	13	5	0.38	0.11	0.47	0.41	0.29
12	1740	19.3	350	731.4	6.1	6.3	495	160	m	24	21	12	0.57	0.55	0.67	0.66	0.71
13	1700	18.2	400	599.2	12.3	5.6	445	74	m	30	24	10	0.42	0.24	0.57	0.50	0.50
14	1700	18.1	500	445.8	14.5	5.7	455	73	363	29	25	7	0.28	0.19	0.55	0.52	0.35
15	1700	18.1	550	487.4	15.6	5.3	399	79	383	30	22	12	0.55	0.24	0.57	0.46	0.60
16	1700	18.1	500	277.8	16.3	5.4	389	71	405	28	25	11	0.44	0.44	0.53	0.52	0.55
17	700	23.2	500	745.0	6.8	5.8	313	185	267	23	18	12	0.67	0.47	0.53	0.64	0.40
18	700	23.0	400	866.0	5.6	6.0	354	200	m	22	14	11	0.79	0.24	0.51	0.50	0.37
19	700	23.4	400	572.8	7.5	6.9	331	210	269	28	18	11	0.61	0.07	0.65	0.64	0.37
20	700	23.3	2500	749.8	6.5	6.6	313	250	246	22	12	17	1.42	0.48	0.51	0.43	0.57

Note: m, Missing values. Abbreviations: Alt, altitude; Temp, temperature; DW, dry weight; OM, organic matter. Diversity values are defined in the text.

Table 3. Environmental and Diversity Parameters of the Five Sites

Alt	ST	STl	STs	STs/STl	Cs	β(ls)	β(l)	β(s)
2550	42	37	16	0.43	0.42	1.57	1.61	2.21
2100	39	35	10	0.29	0.27	2.05	2.22	2.86
1740	36	32	17	0.53	0.53	0.97	2.10	2.62
1700	53	48	20	0.42	0.44	1.88	2.09	2.22
700	43	28	30	1.07	0.52	1.89	1.93	2.55

Note: β(ls) = ST/(mean(Sls) − 1); β(l) = STl/(mean(Sl) − 1); β(s) = STs/(mean(Ss) − 1).

Table 4. Sørensen Measure of Similarity Between the Five Sites for Litter (STl), Soil (STs), and Soil + Litter (ST)

Altitudes	Δ(alt)	CsST	CsSTl	CsSTs
2550–2100	450	0.57	0.14	0.38
2550–1740	810	0.31	0.23	0.30
2550–1700	850	0.46	0.21	0.33
2550–700	1850	0.28	0.28	0.22
2100–1740	360	0.45	0.03	0.30
2100–1700	400	0.46	0.02	0.47
2100–700	1400	0.32	0.03	0.30
1740–1700	40	0.54	0.50	0.43
1740–700	1040	0.35	0.27	0.30
1700–700	1000	0.38	0.39	0.40

2. Habitat diversity corresponds to the number of species at each site, in litter (STl), soil (STs), and litter + soil (ST) (Table 3).
3. Between-sample and between-habitat diversity (≈β diversity) is examined as given below:

   a. Vertical (between-soil layer) diversity is measured at each sample point by the ratio Ss/Sl and Sørensen's index of similarity (Cs = 2 · S[ls]/(Ss + Sl) with S[ls] = number of species shared by soil and litter at a sample point) (Table 2); corresponding measures are given for each site (Table 3).

   b. Horizontal diversity is considered at two scales: between samples on a given site and between sites. The representativeness of each sample relative to its habitat is given by the ratios Ss/STs and Sl/STl; similarly, Sls/ST measures the representativeness of a sample point relative to its sample site (Lauga and Joachim, 1987) (Table 2). Within-habitat diversity is evaluated by the ratios ST/(mean(Sls)-1), STl/(mean(Sl)-1), and STs/(mean(Ss)-1) (β_w of Whittaker, 1960) (Table 3). Between-habitat similarity is estimated by Sørensen's index between sites (Table 4).

E. Data Analysis

Simple Spearman rank correlations (Spearman ρ) between environmental variables and diversity parameters were computed on a microcomputer Macintosh SE30 using the Exploratory Data Analysis package Data Desk v.3 (Velleman, 1988).

Table 5. Spearman Rank Correlations Between Environmental Parameters

	Alt	Temp	CO_2	DW	OM	pH	Coarse	Silt
Temp	−0.89[a]							
CO_2	−0.40	0.23						
D.W.	−0.73[a]	0.81[a]	0.05					
O.M.	0.70[a]	−0.84[a]	−0.13	−0.90[a]				
pH	−0.74[a]	0.88[a]	0.11	0.84[a]	−0.87[a]			
Coarse	−0.55[b]	0.63[a]	0.10	0.62[a]	−0.85[a]	0.72[a]		
Silt	−0.74[a]	0.89[a]	0.29	0.81[a]	−0.80[a]	0.82[a]	0.50[b]	
Clay	0.40	−0.65[a]	−0.16	−0.68[a]	0.76[a]	−0.64[b]	−0.52[b]	−0.80[a]

Note: N = 20 sample points, 1 missing case for DW, 3 missing cases for clay. Abbreviations as in Table 2.

[a] $g < 0.01$.
[b] $g < 0.05$.

III. RESULTS

A. Collembolan Fauna

From 63 genera of Collembola 112 species were recognized, with a total of 3586 individuals. The high species richness and low population densities, compared to those of temperate forests, are consistent with our previous observations on the Collembolan communities in the upper part of the Doi Inthanon (Deharveng et al., 1989). Although Doi Inthanon now has the best known Collembolan fauna in tropical Asia (Yosii, 1961; Deharveng, 1987, 1989; Bedos and Deharveng, 1990), 85 out of these 112 species are new to science.

B. Correlations Between Habitat Parameters (Table 5)

Altitude and temperature were strongly linked, as expected, despite some discrepancy for the disturbed site at 1740 m where the forest had been partially cleared. Both factors were also significantly correlated with all other parameters, except CO_2 (with altitude and temperature) and clay (with altitude), probably as a result of present bioclimatic conditions and pedogenesis (Figure 1). Each factor is therefore a fairly good predictor of the main habitat characteristics. On the other hand, to infer causal connections from observed correlations between a given abiotic factor and diversity parameters is difficult. No correlation was observed between carbon dioxide and any other abiotic parameter, but records of CO_2 were fairly imprecise, because of technical problems inherent to this kind of measurement in the field. The value 4–8 times higher than others obtained at sample point 20 was not associated to similarly outlying values in other parameters (Table 2).

C. Relation of Point Diversity to Habitat Parameters

Species richness of litter samples, soil samples, and sample points were subjected to correlation analyses with the nine environmental parameters. A few

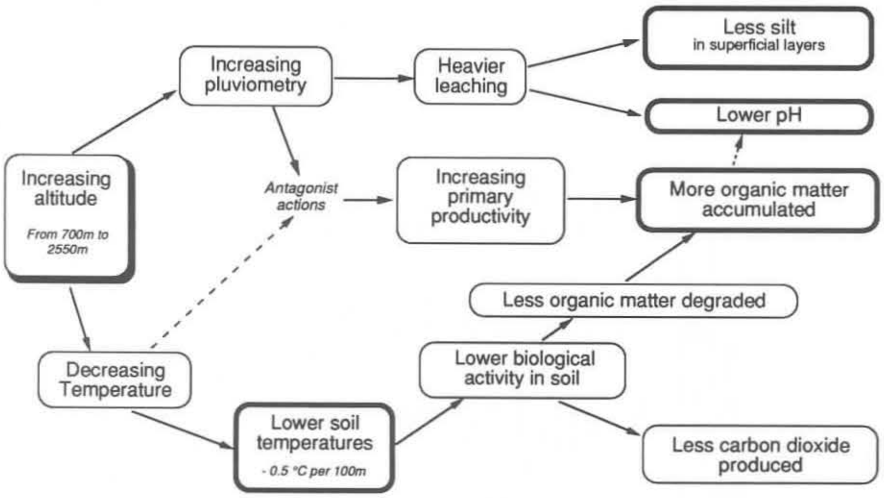


Figure 1. Influence of altitude on some soil abiotic parameters in Doi Inthanon. Thickened frames indicate that the parameter was found highly correlated to altitude in our data.

significant correlations were obtained: Sls and Sl with silt and clay; Sl with temperature and organic matter; Ss with altitude, temperature, and dry weight (Table 6). On the whole, these correlations were much lower than the correlations between abiotic parameters.

Because of the loss of its forest cover, the 1740-m site shows a significant shift in the values of some environmental parameters, in particular, a low organic matter content relative to altitude and temperature. Situated on a steeper slope than the other sites, the 2100-m site is characterized by severe soil erosion and gullies with a patchier litter cover. These features, not taken into account in the analyses, introduced a bias in the results. To reduce such distortions, the correlation analyses were conducted with each site discarded in turn (partial analysis). If the 2100-m site was omitted, the species richness of litter showed highly significant correlations with most abiotic variables (but not with altitude, Table 6 and Figure 2). If the disturbed 1740-m site was left out, the relationship of abiotic factors to soil species richness was significantly improved (Table 6 and Figure 2). In particular, there is a clear disparity between the soils at 700 and 1700 m and those at 2100 and 2500 m. The latter, in spite of a much higher organic matter content (41.7 ± 9.8 against $10.6 \pm 4.5\%$, difference statistically significant at $p < 0.01$ with 14 df), carry a noticeably less diverse fauna (6.4 ± 2.4 against 11.4 ± 2.8 species per sample, a difference statistically significant at $p < 0.01$ with 14 df).

Some relationship exists, therefore, between species richness and environmental parameters studied in this work, and more extensive sampling would probably have established this more firmly, as demonstrated by some non-

Table 6. Spearman Rank Correlations Between Environmental and Diversity Parameters

	Alt	Temp	CO_2	DW	OM	pH	Coarse	Silt	Clay
Global analysis[a]									
Sls	−0.01	−0.26	−0.12	−0.21	0.42	−0.15	−0.24	−0.46[b]	0.73[c]
Sl	0.29	−0.52[b]	−0.24	−0.42	0.54[b]	−0.32	−0.27	−0.67[c]	0.78[c]
Ss	−0.58[b]	0.48[b]	0.00	0.50[b]	−0.21	0.39	0.03	0.30	0.25
Ss/Sl	−0.70[c]	0.72[c]	0.00	0.67[c]	−0.53[b]	0.61[c]	0.25	0.62[c]	−0.20
Sørensen	−0.22	0.26	−0.16	0.42	−0.24	0.27	0.13	0.11	0.00
Sls/ST	0.29	−0.35	−0.34	−0.25	0.50[b]	−0.17	−0.45[b]	−0.38	0.56[b]
Sl/STl	0.20	−0.19	−0.47[b]	−0.12	0.33	−0.03	−0.36	−0.27	0.37
Ss/STs	0.11	−0.16	−0.04	−0.05	0.31	−0.11	−0.28	−0.15	0.44
Without 2100 m[d]									
Sl	0.43	−0.74[c]	−0.19	−0.79[c]	0.82[c]	−0.69[c]	−0.35	−0.86[c]	0.78[c]
Ss	−0.60[b]	0.44	0.25	0.42	0.06	0.12	−0.27	0.39	0.33
Without 1740 m[e]									
Sl	0.42	−0.43	−0.29	−0.30	0.40	−0.12	−0.03	−0.67[c]	0.76[c]
Ss	−0.65[b]	0.64[b]	0.16	0.60[b]	−0.60[b]	0.67[c]	0.32	0.43	−0.04

Note: Abbreviations as in Table 2.

[a] N = 20 sample points, 1 missing case for DW, 3 missing cases for clay.
[b] g < 0.05.
[c] g < 0.01.
[d] N = 16 sample points, 1 missing case for DW, 3 missing cases for clay.
[e] N = 16 sample points, 2 missing cases for clay.

standardized samples not analyzed here. However, correlation patterns are complex; soil and litter, in particular, behave quite differently in this respect.

D. Between-Layer Diversity

In four out of the five study sites, the number of Collembolan species in the soil layer was less than 55% of that in litter; in the fifth site (700 m), the richness was similar (30 species in soil and 28 in litter). On the scale of sample points, all litter samples but one yielded more species than the corresponding soil samples (Table 2). The higher diversity of litter communities, already well documented for most edaphic groups of Arthropods (Delamare Deboutteville, 1951; Hagvar, 1983), is therefore verified in our data.

Globally, 55 species were collected in soil against 103 in litter, for a total of 112 species; thus, only 9 out of the 55 soil species were not present in litter. This large overlap in faunistic composition between the two habitats decreases at the sample scale, and usually less than half of the soil species were shared with overlying litter at any single sample point. Soil communities are therefore not merely impoverished litter communities, but rather unique assemblages of species as was also observed by Ponge (1980) in temperate forests. The low values of the Sørensen similarity index at sample points (Table 2) and the low correlation between Ss and Sl (Spearman $\rho = 0.18$) support this view. The disparity between the high global similarity of soil and litter faunas, and the clear vertical differentiation at each sample point and each site might result from sampling bias, since the fauna of the thin ecotone zone between soil and litter layer is always partly included in both habitat samples.

The factors that relate most significantly to diversity in litter (silt and clay) are only poorly related to diversity in soil. Altitude is significantly related to soil, but not to litter diversity. Even more unexpected is the opposite relation of most abiotic factors to diversity in litter vs diversity in soil. As a consequence, correlations between the ratio Ss/Sl and six out of the nine environmental factors were found to be significant or highly significant (Table 6). Similar results were obtained from partial analyses.

While CO_2 does not show a significant correlation with any of the diversity measures, the only sample where Collembolan species were more numerous in soil than in litter also recorded the highest CO_2 level. Such isolated spots of high carbon dioxide production were found occasionally in forest litters in Thailand and Sulawesi, associated with large amounts of mycelium (unpublished observations). Whether this always influences community richness in the way suggested by the present data is not known.

E. Soil Layers Vs Site Differentiation

Species collected at one sample point of a given site represented 36–74% of the total number of species collected at that site (the ranges were 34–70% for litter and 29–71% for soil, respectively). The range of representativeness of

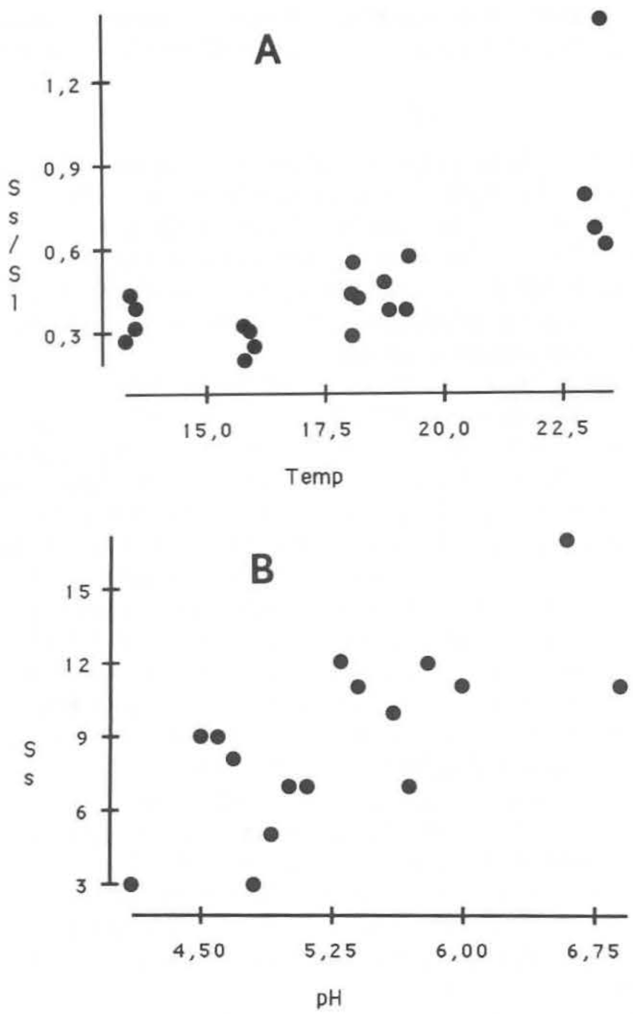
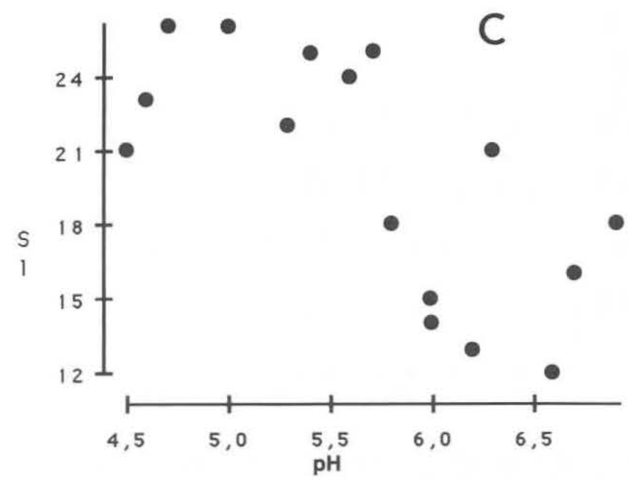


Figure 2. Plots of different diversity measures against abiotic factors. (A) Global analysis (soil species richness/litter species richness) against temperature; (B) partial analysis (without the 1740-m site), soil species richness against pH; (C), (D): partial analyses (without the 2100-m site), litter species richness against pH and dry weight.

litter samples was either similar to, or narrower than, that of soil samples at a site; and these ranges largely overlapped except at the 2550-m site (Figure 3). These differences might result from a more aggregated horizontal distribution of Collembola in soil than in litter, a hypothesis which could be tested in a larger number of samples.

Between-site similarity measured by the Sørensen coefficient (Table 4) was higher in soil than in litter, except for 1740 vs 1700 and 2550 vs 700. Collembolan



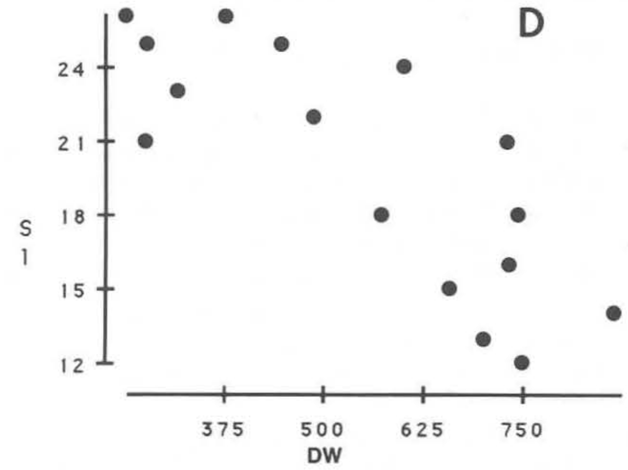


Figure 2 (continued).

communities from site to site thus were less different in soil than in litter, probably in relation to a lower differentiation of soil habitats at this scale.

F. Altitudinal Gradient

Most abiotic factors exhibit a clear, monotone relationship with altitude from 700 to 2550 m. One might expect parallel changes in soil animal communities to occur. Faunal composition does undergo such conspicuous changes, but pattern is less clear for diversity itself. Progressive species replacement occurs from 700 to 2550 m, with a discrepancy for the disturbed 1740-m site; this process results in a decreasing similarity between increasingly distant sites (Table 4). The 2550-m site shows, however, much less similarity to the 1740-m site than to the 1700-m

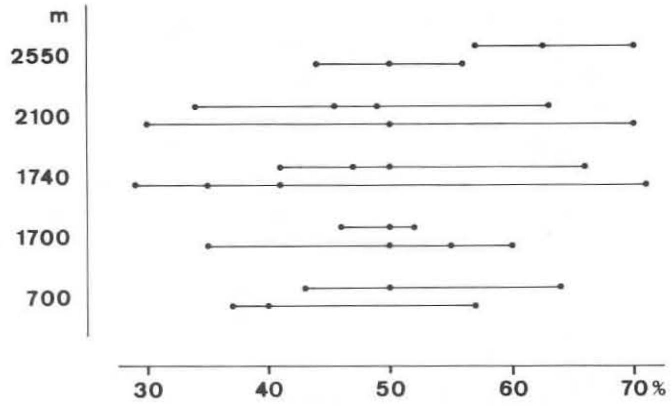


Figure 3. Range of correlation of sample species richness relative to site species richness for litter (upper bar) and soil (lower bar).

site, because of the loss of montane forest species as a result of clearing at 1740 m.

As regards diversity, no relationship is apparent between altitude and species richness of sample points or sites, but soil/litter differentiation is clearly related to elevation (Table 6). Thus, our data again provide contrasting evidence for altitudinal gradients in diversity with respect to the soil compartments analyzed. Although elevational gradients in diversity are well known in many organisms (Pianka, 1966; McCoy, 1990), their precise patterns are not simple when analyzed in detail. For instance, in a study of Andean bird diversity, Terborgh (1977) found that the global number of species decreased parallel to elevation, but if component trophic categories were examined, one out of three of these categories did not respond to the gradient. This is also true for the Collembola on Doi Inthanon, because communities of contiguous, closely related habitats (soil and litter) behave in an almost opposite way with altitude. This independent behavior of litter and soil communities has already been discussed by Dunger (1975), working on temperate ecosystems; according to this author, soil communities respond to substrate properties whereas litter communities respond to vegetation.

G. Habitat Heterogeneity

Habitat heterogeneity can be estimated by the between-sample variations of the different abiotic parameters recorded. On the whole, abiotic factors, particularly temperature and pH, showed little variation at a given site. No significant correlation was found with any diversity measure, but merely examining the data brought interesting information to light. The most ''heterogenous'' site for most parameters (2100 m) had the lowest number of soil species; its β diversity (Table 3) was also higher than that of other sites. Conversely, the highest habitat diversity ST (at 1700 m) corresponded to the highest variations of dry weight. These

contrasting results do not support a clear dependence of diversity on abiotic heterogeneity, but the data are still too scant to make any firm conclusion. We would just like to point out that heterogeneity may act differently on diversity according to its origin. Some kinds of heterogeneity (such as the patchy distribution of litter at the 2100-m site) may be derived from disturbance of the habitat, whereas others (such as variations in soil porosity or vertical differentiation in the soil structure) are obviously the result of a long-term evolution of the habitat. Because of the poor dispersal and recolonization ability of soil animals, disturbance heterogeneity usually lowers diversity. The other kind of heterogeneity has in common with complexity that it is dependent on habitat stability and tends to enhance diversity.

IV. CONCLUSIONS

A. General Patterns of Diversity

Diversity patterns emerging from our data are complex. They are not explained at present by any dominant environmental parameter; instead, different factors are correlated to different aspects and different scales of the diversity observed. Some (such as pH or porosity) may act directly on community organization and diversity, while others (such as silt) are probably only parallel effects of the same underlying cause. None of these factors was found to be a good predictor of Collembolan diversity at a given sample point. We interpret this failure as reflecting the complex determinism of diversity in soils; keep in mind, however, that important abiotic factors such as soil stability, soil hydric properties, and chemical factors other than pH were not considered in the present chapter.

Diversity patterns became less confusing if litter and soil were dealt with separately in the analyses. The vertical stratification of soils in successive layers, corresponding to different stages of decomposition and alteration, has long been recognized as a major structuring factor in soil animal communities (Wallwork, 1976). The largely different response of soil and litter diversities to environmental factors and gradients was, however, unexpected.

B. Classical Hypotheses of Species Diversity

The productivity hypothesis (Pianka, 1966; Brown, 1981), as a tentative explanation of diversity patterns, relates species diversity to the production of trophic resources, which are fungi and microorganisms for most Collembola. Carbon dioxide level in the litter and organic matter content of the soil provided indirect estimates of this parameter. Correlations with diversity measures were usually low (Table 6). If the disturbed site of 1740 m was discarded, organic matter-rich sites (mor-type of 2550 and 2100 m) showed, however, significantly lower diversity in soil than organic matter-poor sites (at 1700 and 700 m). Productivity hypothesis could be relevant here if the formation of humus with increasing elevation changed from a mostly biological to a mostly biochemical

process as suggested by Bailly (personal communication, 1990): microorganisms would decrease in density with altitude, conversely to the accumulation of raw humus. Organic matter content would therefore represent a poor estimator of the available trophic resources for Collembola in the soil. Further investigations are obviously needed to clear these points.

The complexity-heterogeneity hypothesis relates diversity to the structural heterogeneity of the habitat (Giller, 1984). Resources diversity is usually a major component of this heterogeneity; thus, the preceding discussion about productivity is, in part, relevant here (assuming that a relation exists between the amount and the diversity of trophic resources in a tropical rain forest). Higher resource diversity and narrower partitioning of the trophic dimension of the niche are considered to increase species diversity. The problem is that no reliable evidence of strict trophic specialization has been found in most soil Arthropods, including Collembola (Petersen, 1971; Anderson, 1975; Greenslade and Greenslade, 1983). Soil species can be easily assigned either to sucking species, or predominantly geophagous (? bacteria feeders) species, or predominantly fungus/plant feeders; however, inside these broad trophic categories, only slight preferences are usually observed between species (Vannier, 1979; Arpin et al., 1980). Furthermore, the tiny differences in trophic requirements that have been established so far from observations and experiments concern a few isolated species. But, do Collembolan species specialize their diets when they are packed together in the same community? In an attempt to answer this question, we compared the gut content of different species and individuals occurring in the same 500-cm^3 sample of litter from Doi Inthanon at 2550 m. Preliminary results showed that a large variety of elements were present in the guts. The three large trophic categories mentioned above were recognized. Conversely, no clear differences were observed in gut contents between species of the same trophic category. Even if narrow trophic specialization can be expected in some sucking groups (Greenslade and Greenslade, 1983), the bulk of the fauna does not show such a trend, as far as ingested elements are concerned (Ponge, 1988).

We did not measure resource diversity in soils directly, but data are available for vegetation. The reduction with altitude in number of tree species on the Doi Inthanon mountain (Robbins and Smitinand, 1966; Koyama, 1984), which should result in a parallel decrease in the diversity of nutrients at the litter level, is not associated with a reduction in number of litter species per sample (whereas diversity in soil decreases along this gradient, probably in relation to other parameters). As a consequence, heterogeneity in trophic resources is likely to play only a minor role in the regulation of soil species diversity in the altitudinal range studied, and the absence of clear patterns relating it to estimates of trophic resources of the habitat is not surprising.

Heterogeneity in other dimensions of the niche led us to recognize, as a working hypothesis, the existence of two kinds of heterogeneity: disturbance heterogeneity and complexity heterogeneity, which should have an antagonistic influence on diversity as far as soil Collembola are concerned. Future investigations should pay special attention to such soil heterogeneity patterns.

C. Perspectives

More interesting insights might be gained from the consideration of abundance distribution of the species in the samples or habitats. For the present time, however, it would be premature to speculate much further about the determinants of diversity in tropical soil communities for three main reasons:

1. Soil is a highly complex system (Lavelle, 1984), probably more difficult to subdivide into well-defined components than any other terrestrial system. Integrated sets of abiotic and biological data would therefore be necessary to draw firm conclusions.
2. Information available on biological diversity obtained from well-known epigean communities can be extrapolated only to a limited extent to the soil system. In particular, fundamental differences between soil and epigean communities exist at the trophic level, which is often advocated to account for diversity patterns.
3. Finally, so little is known about life in tropical soils that sound, standardized data collections on the specific composition of the communities appear to be the immediate and central need for further progress in the field of soil biological diversity patterns.

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